Abstract. Fully understanding the importance of zebra and quagga mussels’ effects on internal nutrient (especially nitrogen and phosphorus) cycling in large lakes like Lake Erie is essential when attempting to ameliorate their contribution to beneficial use impairments and to understand how invasive species perturb ecosystems in their invasive ranges. Here, we first used field surveys to determine the current (2004) dreissenid community structure on hard, preferred substrate in the western basin of Lake Erie. We then estimated the potential nutrient subsidy to the phytoplankton community by dreissenid nitrogen and phosphorus excretion by integrating the dreissenid community structure at these sites with published size-specific nutrient excretion regressions. We found that the total dreissenid community density had decreased dramatically (by > 50%) from previous estimates, that zebra mussels now comprised only a small fraction of the total density (< 3%), and that the quagga mussel-dominated community could supply up to 50% of the nitrogen and 3% of the phosphorus needed daily by the phytoplankton community. The findings emphasize (1) that the dreissenid community abundance and composition are not static, (2) that zebra mussels are no longer more important than quagga mussels to the dreissenid community, and (3) that dreissenid mussels potentially supply a portion of the nutrients that stimulate phytoplankton growth in the western basin of Lake Erie, making them important contributors to nutrient cycling in addition to their role as consumers of phytoplankton.
Activities and timelines. Work on this project began with field sampling in June 2004, continued through 2005-2007 with laboratory analysis of the samples and data, and ended in late 2007 with preparation of the project report. Here, we briefly summarize project activities. During 2004, field sampling at 10 established western Lake Erie stations occurred in June with several sites sampled again in October 2004, although not all stations were visited in October due to inclement weather. Over the course of the project, we employed three undergraduate students that assisted with processing of field-collected samples. The project took longer than anticipated because the first undergraduate student participant left to attend graduate school. The other two students were recruited to assist with processing of the field samples at a later time. Further, the large number of samples to be processed (>5,700 mussels in the length-weight analyses and >11,000 in the length-frequency analyses, respectively) lengthening the duration of the project.

Introduction

Beneficial use impairments, including degradation of the benthos, excessive “undesirable” algal growth, degradation of aesthetics, degradation of zooplankton and phytoplankton communities, and loss of fish habitat, continue in Lake Erie due to the recurrence of cyanobacterial blooms (Conroy et al. 2005b) and hypolimnetic hypoxia (Burns et al. 2005). Impairments persist despite efforts stretching over three decades and costing well over $1 billion to limit these problems. These continued problems indicate either the presence of a persistent perturbation that has not been remedied or the occurrence of new perturbations after some problems have been corrected.

One such “new” perturbation in Lake Erie is the invasion of dreissenid mussels (first the zebra mussel, *Dreissena polymorpha*, Hebert et al. (1989), followed by the quagga mussel, *D. bugensis*, May and Marsden 1992). Dreissenid mussels were first hypothesized to affect Lake Erie function through consumptive mechanisms (MacIsaac et al. 1992, Bunt et al. 1993, Nicholls and Hopkins 1993), potentially limiting the flow of energy from primary producers to the upper trophic levels (MacIsaac 1996b). Other studies propose that selective feeding by dreissenids may facilitate cyanobacterial blooms (Vanderploeg et al. 2001); others indicate the opposite trend (Dionisio Pires and Van Donk 2002). However, dreissenid mussels may also facilitate cyanobacterial blooms by serving as nutrient remineralizers (Conroy et al. 2005a). That is, dreissenid mussels in the benthos intercept particles (either living or dead phytoplankton or other detrital particles) that have either settled or been mixed down to the benthos, consume them, and then excrete some portion of the nutrients that would have otherwise ended up in the sediments back into the water column. We have previously estimated the magnitude of this effect for a site in the western basin and found that dreissenid mussels potentially excrete twice as much ammonium-nitrogen (54.8 vs. 23.9 mg NH₄-N m⁻² d⁻¹) but one-quarter as much phosphate-phosphorus (3.2 vs. 11.2 mg PO₄-P m⁻² d⁻¹) as does the crustacean zooplankton community in the water column (Conroy et al. 2005a). However, our finding was limited to one particular site in the absence of dreissenid density data from throughout the western basin from which to estimate the effect of dreissenid density data from throughout the western basin from which to estimate the effect of dreissenid density data from throughout the western basin from which to estimate

Here, we use a basin-wide survey of the abundance and size-frequency of dreissenids from their preferred, hard substrate sites to test (1) whether densities and size-frequency distributions are similar throughout the western basin, (2) whether quagga mussels have replaced zebra mussels, and (3) the importance of dreissenid mussels in supplying nutrients to the phytoplankton
community. We found that densities and size-frequency distributions varied both spatially and temporally (within one growing season), that the dreissenid community is now nearly completely dominated by quagga mussels, and that dreissenid mussels were more important in supplying nitrogen than phosphorus to the phytoplankton community.

Methods

Field sampling and laboratory processing

To determine the current dreissenid community structure (including the abundance of zebra vs. quagga mussels and their size-frequency distributions), we surveyed 10 sites located throughout the western basin (Fig. 1) during June and October 2004. These 10 locations represent sites of hard, preferred habitat which is rarely surveyed (Pontius 2000, Patterson et al. 2005), yet for which previously published data on dreissenid community structure are available. Four sites (Bay Point, Gull Island Shoal, Niagara Reef, and Peach Point, Table 1) were sampled previously by Pontius (2000), and our laboratory group has regularly surveyed Peach Point, South Bass Island since 1991 (Pontius 2000, Conroy et al. 2005a). This site was initially dominated by small (< 15 mm) zebra mussels, and density (both abundance and biomass) increased rapidly after initial colonization followed by a decline and stabilization at about 20,000 ind. m⁻² (Pontius 2000, Conroy et al. 2005a). The other sites (Table 1) included those at or near the Chicken Island complex (Hen Island and Little Chicken Island, Griffiths et al. 1991; Sunken Chicken Reef, Fitzsimmons et al. 1995; North Harbor Island, Ackerman et al. 2001), one near the middle of the basin (Middle Sister Island, Ontario, Griffiths et al. 1991, Maclsaac 1996a), and one near the central basin (Chickenolee Reef, Griffiths et al. 1991).

Working from F.T. Stone Laboratory (Put-in-Bay, Ohio) aboard the R/V Erie Monitor, divers collected all mussels from three random, replicate quadrats (ranging from 0.06 to 0.25 m² depending on mussel density) at each site (depth > 4.0 m), put the contents into pre-labeled containers, and placed the mussels on wet ice in the field. Upon returning to the field station, samples were frozen (-20 °C) and then transported to laboratory facilities at The Ohio State University (Columbus, Ohio). Once in the laboratory, mussels were thawed and all mussels collected in a quadrat were identified to species according to Domm et al. (1993) and enumerated. Up to 500 mussel lengths from a quadrat sample were measured to the nearest 0.1 mm with vernier calipers and soft tissue was removed. Dry soft-tissue biomass was determined for up to 200 mussels from each quadrat sample by drying at 60 °C to constant weight in pre-weighed foil pans.

Determining the dreissenid community size structure and nutrient cycling effects

From measured lengths, we constructed length-frequency diagrams to determine the size structure of the dreissenid community. We did not construct species-specific size-frequency diagrams as previous studies have done (e.g., Pontius 2000, Conroy et al. 2005a) as < 3% of the mussels identified in our samples were zebra mussels (see Results and Discussion). Combining length and dry weight data, we then constructed site-specific and combined-site length-weight models using linear regression (Microsoft Excel, Redmond, Washington). To estimate the potential effect of the dreissenid community on nitrogen and phosphorus cycling, we calculated
site-specific dreissenid community nitrogen (mg NH₄-N m⁻² d⁻¹) and phosphorus (mg PO₄-P m⁻² d⁻¹) excretion rates by combining the size-frequency distributions determined in this study and the nutrient excretion regression models of Conroy et al. (2005). We used the combined-species nitrogen excretion rate equation and the quagga mussel phosphorus excretion rate equation because zebra mussels were a minor fraction of the dreissenid community at all sites. Upon calculating length-weight regression models for our sites, we noticed that our models generally gave individual biomasses greater than those reported by Pontius (2000) and Conroy et al. (2005a), especially for larger mussel sizes. To assess the importance of these “larger” mussels, we estimated individual biomass from the length-weight model for quagga mussels reported in Conroy et al. (2005a; \( W = 7.8 \times 10^{-6} L^{2.78} \)) and the combined-site length-weight model from this study (\( W = 1.47 \times 10^{-5} L^{2.99} \)) in addition to the site-specific length-weight model used above and in turn re-calculated site-specific dreissenid nitrogen and phosphorus excretion rates. We then calculated a site-specific mean nutrient excretion rate by determining the arithmetic mean of these three rates (from the three methods of estimating individual mussel biomass). Overall, it appeared that the dreissenid density (ind. m⁻²) was more important than the difference between biomasses in the areal excretion rate calculation (see Results and Discussion). We then compared these nutrient “supply” rates with phytoplankton “demand” rates determined from the western basin Lake Erie nitrogen- and phosphorus-debt (mmol nutrient mg chlorophyll⁻¹ d⁻¹) determinations and chlorophyll \( a \) concentrations (mg chlorophyll m⁻³) reported by Guildford et al. (2005).

**Results and Discussion**

**Dreissenid community structure: size-frequency, density, and length vs. weight**

Dreissenid community structure displayed various patterns among the 10 sites sampled. At most sites, larger (> 15 mm) mussels were prevalent (Fig. 2). At a smaller number of sites, smaller mussels were most frequently encountered (Fig. 2). Most sites only had one peak in the frequency distribution (Fig. 2) indicating the presence of only one year class (Griffiths et al. 1991) although distributions were rather long-tailed towards smaller size classes. The extremely small mussels either were not present, potentially due to round goby predation (Diggins et al. 2002), or were missed by our sampling or processing methods.

Dreissenid densities were at least 50% lower than previous estimates at these sites (e.g., all-site mean = 3,838 ind. m⁻², SE = 1142; cf. Conroy et al. 2005a, Pontius 2000) and zebra mussels had nearly been extirpated (all-site mean % = 2.3). Remarkably, sampling in May 2003 at Peach Point revealed a total density of 20,847 ind. m⁻²; in June 2004, density had dropped to 4,224 ind. m⁻². Although the SE of the 2004 measurement approached 25% of the mean, we cannot immediately explain the remaining loss of mussels. Contemporaneously, mussels had greater biomasses in 2004 for the same length than in previous years (Fig. 3; cf. Pontius 2000, Conroy et al. 2005a). Consequently, there appears to be some indication of relaxation of exploitative competition among mussels as zebra mussels are lost from the community. Perhaps this indicates a minimization of intra-specific competition as the benthic community becomes dominated by a single mollusk species, although the mechanisms for identifying neighbors as similar species and minimizing competition are completely unknown. By October 2004, densities were similar to those in spring at all sites sampled (i.e., all except Hen Island, Middle
Sister Island, North Harbor Island, and Sunken Chicken Reef sites, which were not sampled due to weather), (all-site mean = 4,247 ind. m\(^{-2}\), SE = 1,495 excluding Chickenolee Reef where mean density = 28,885 ind. m\(^{-2}\)). Zebra mussels remained a low portion of the dreissenid community (all-site mean = 2.1\%). In the October samples, however, small mussels (< 15 mm) were much more prevalent (Fig. 3) than in spring, indicating recruitment to the community.

At all sites, weight increased as a power function of length as has been found in numerous previous studies (Jarvis et al. 1998, Pontius 2000, Conroy et al. 2005a, Patterson et al. 2005). However, the slope (exponent) of the power function varied among sites (Fig. 4) potentially indicating different physiological status among sites. The highest slope was found at a site (Bay Point) where the hyper-eutrophic Sandusky Bay (Conroy et al. 2007) discharges into Lake Erie (Fig. 1), potentially indicating an increased organic matter supply to the dreissenid community. Similar slopes were found at the Chicken Island complex (slope = 2.97, 2.89, and 2.98 at Hen Island, Little Chicken Island, and Sunken Chicken Island, respectively). Merging all the data formed a well-supported model (Fig. 5) that had an intercept qualitatively similar to that of Patterson et al. (2005; \(a = 1.66 \times 10^{-5}\)). Our slope was somewhat greater than Patterson et al.’s (2005; \(b = 2.46\)) although they did not include any western basin mussels in their determinations due to the difficulty of collecting mussels with a PONAR dredge on rocky substrates.

**Dreissenid community potential effects on nitrogen and phosphorus cycling**

Depending on the site and the particular community composition at that site, the dreissenid community may supply >50% of the daily nitrogen demand of the phytoplankton community but < 3% of its daily phosphorus demand at our 10 sites (Fig. 6). These values, especially the phosphorus supply value, may seem insignificant, except that these nutrients most likely would have ended up in the sediments, either being turned over on a much longer time scale due to bacterial decomposition or other processes, or have been removed completely from possible reuse with sediment burial. Consequently, we argue here, as we did in Conroy et al. (2005a), that dreissenid mussels play an important role supplying nutrients, especially nitrogen, to the phytoplankton community. Further, it is important to consider whether the effect of mussels is primarily an outcome of their extreme density, their size structure, or their species-specific makeup. We have previously argued that species-specific makeup matters little (Conroy et al. 2005a) as communities that were 75% zebra mussels (e.g., those of 1998) or 75% quagga mussels (e.g., those of 2003) quickened nutrient turnover times similarly. Because the dreissenid community is now nearly 100% quagga mussels (see above), community composition need not be considered in Lake Erie. Conroy et al. (2005a) conclude that mussel density considerably affects the amount of nutrients supplied to the phytoplankton. We concur with that assessment. Relating community excretion rates to mean site densities, > 92% of the variation in excretion rates was explained (Fig. 6). Importantly, the one site that appeared to deviate from this model (Bay Point: mean density = 5,920 ind m\(^{-2}\), mean estimated N excretion rate = 15.3 mg NH\(_4\)-N m\(^{-2}\) d\(^{-1}\), predicted rate = 27.7; mean P excretion rate = 0.7 mg PO\(_4\)-P m\(^{-2}\) d\(^{-1}\), predicted rate = 1.2) was composed almost exclusively of individuals < 15 mm (Fig. 2), and Conroy et al. (2005a) showed that larger mussels have greater biomass-corrected excretion rates than do smaller individuals. The strength of these density-specific excretion rate models indicates that nitrogen and phosphorus excretion by the dreissenid community can be quickly estimated for hard substrates in the western basin for which dreissenid densities are known.
In conclusion, we investigated how dreisseind community structure (species composition, density, and size-frequency distribution) varied across the hard, preferred substrate in the western basin of Lake Erie in 2004. We found important differences in community structure including the nearly complete absence of zebra mussels. We combined the length-frequency distributions from our 10 sample sites with published nutrient excretion models (Conroy et al. 2005a) to estimate the dreissenid community’s contribution to the nitrogen and phosphorus available to the phytoplankton community. We found that the dreissenid community may supply up to 50% of the nitrogen but < 3% of the phosphorus needed by the phytoplankton daily, although the rate of delivery of the nutrients to the euphotic zone is limited by the hydraulic mixing of the water column (Edwards et al. 2005).

Literature Cited


Table 1. Published length-frequency and/or density information for the 10 sites sampled in this study including the year sampled and dreissenid density (in thousands m$^{-2}$) when reported in the published study. For Peach Point in 1998 and 2003, the number before the forward slash is the zebra mussel density and the number after is the quagga mussel density. Densities for Bay Point, Gull Island Shoal, and Niagara Reef are mean values of those densities given in Table 4 of Pontius (2000). Sites are described in the original sources. Note that empty density cells indicate no summarized data were reported in the original citations.

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Figure Captions.

Fig. 1. Map of the western and part of the central basins of Lake Erie showing the dreissenid community sampling sites (filled circles) and depth contours (solid lines). Site location abbreviations are: BP = Bay Point, COL = Chickenolee Reef, GI = Gull Island Shoal, HI = Hen Island, LCI = Little Chicken Island, MSI = Middle Sister Island, N = Niagara Reef, NHI = North Harbor Island, PP = Peach Point, and SCI = Sunken Chicken Reef. Water depth contour interval = 5 m.

Fig. 2. Length (mm)-frequency (% of density) distribution in 0.5-mm intervals of the dreissenid community at 10 sites (a) – (j) in the western basin of Lake Erie from June 2004 collections. Site locations are shown in Fig. 1 and mean densities (of up to three replicate quadrat samples) are indicated.

Fig. 3. Length (mm)-frequency (% of density) distribution in 0.5-mm intervals of the dreissenid community at 10 sites (a) – (j) in the western basin of Lake Erie from October 2004 collections. Four sites could not be sampled due to weather conditions. Site locations are shown in Fig. 1 and mean densities (of up to three replicate quadrat samples) are indicated.

Fig. 4. Weight (g dry weight)-length (mm) models for the 10 sites sampled during June 2004 in the western basin of Lake Erie. The relationships for the three quadrat samples are indicated (1 = circles, 2 = squares, 3 = triangles). Coefficients of the regression model (a = intercept, b = slope), the number of data points (n), and the proportion of the variation explained ($R^2$) are indicated.

Fig. 5. Combined weight-length model for all sites sampled during June 2004 in the western basin of Lake Erie with model coefficients, number of data points, and proportion of the variance explained indicated.

Fig. 6. Site-specific dreissenid community nitrogen (a) and phosphorus (b) excretion rates (mg nutrient m$^{-2}$ d$^{-1}$) versus site-specific mean density for the 10 sites in western basin Lake Erie sampled in June 2004. The intercept (b) and slope (m) of the relationship, number of data points (n), and the proportion of the variance explained ($R^2$) by the model are indicated. Also shown are the nitrogen and phosphorus demands (mg nutrient m$^{-2}$ d$^{-1}$) of the phytoplankton community calculated from data from Guildford et al. (2005).
Fig. 1.
Fig. 3.

(a) Bay Point 10/2004
Mean Dens. = 1792 m²
(b) Chickenolee 10/2004
Mean Dens. = 28885 m²
(c) Gull Island 10/2004
Mean Dens. = 5627 m²
(d) Hen Island 10/2004
Not Determined
(e) Little Chicken Island 10/2004
Mean Dens. = 591 m²
(f) Middle Sister Island 10/2004
Not Determined
(g) Niagara 10/2004
Mean Dens. = 41444 m²
(h) North Harbor Island 10/2004
Not Determined
(i) Peach Point 10/2004
Mean Dens. = 9083 m²
(j) Sunken Chicken Island 10/2004
Not Determined
Fig. 4.

(a) Bay Point
06/2004
\(a = 3.64 \times 10^{-6}, b = 3.64\)
\(n = 437, R^2 = 0.86\)

(b) Chickenolee
06/2004
\(a = 6.17 \times 10^{-5}, b = 2.56\)
\(n = 252, R^2 = 0.57\)

(c) Gull Island
06/2004
\(a = 6.33 \times 10^{-6}, b = 3.32\)
\(n = 227, R^2 = 0.81\)

(d) Hen Island
06/2004
\(a = 1.88 \times 10^{-5}, b = 2.97\)
\(n = 416, R^2 = 0.87\)

(e) Little Chicken Island
06/2004
\(a = 1.70 \times 10^{-5}, b = 2.89\)
\(n = 408, R^2 = 0.47\)

(f) Middle Sister Island
06/2004
\(a = 2.33 \times 10^{-5}, b = 2.80\)
\(n = 479, R^2 = 0.85\)

(g) Niagara
06/2004
\(a = 7.214 \times 10^{-5}, b = 2.31\)
\(n = 236, R^2 = 0.44\)

(h) North Harbor Island
06/2004
\(a = 2.09 \times 10^{-4}, b = 2.15\)
\(n = 91, R^2 = 0.84\)

(i) Peach Point
06/2004
\(a = 1.15 \times 10^{-5}, b = 3.19\)
\(n = 189, R^2 = 0.90\)

(j) Sunken Chicken Island
06/2004
\(a = 1.32 \times 10^{-5}, b = 2.98\)
\(n = 556, R^2 = 0.77\)
Fig. 5.

Length (mm)

Dry Weight (g)

0 5 10 15 20 25 30 35

0.0 0.2 0.4 0.6 0.8 1.0

All Sites
06/2004

\[ a = 1.47 \times 10^{-5}, \ b = 2.99 \]

n = 3291, R² = 0.79
Fig. 6.

(a) Mean N Excretion Rate (mg NH₄-N m⁻² d⁻¹)
- 06/2004
- \(b = 1.21, m = 4.48\)
- \(n = 10, R^2 = 0.92\)
- PP demand = 109 mg N m⁻² d⁻¹

(b) Mean P Excretion Rate (mg PO₄-P m⁻² d⁻¹)
- 06/2004
- \(b = 0.03, m = 0.20\)
- \(n = 10, R^2 = 0.94\)
- PP demand = 83 mg P m⁻² d⁻¹

Mean Density (ind. m⁻² / 1000)
Work products. With Lake Erie Protection Fund support from this small grant, we supported field research activities and laboratory measurements and three undergraduate research assistants at various points during the course of this project. Of note is that one of the undergraduate assistants continued her studies into graduate school (currently at the University of South Florida working on paleoclimate indicators in marine sediments), another will graduate in spring 2008 and is currently applying for graduate school (focusing on programs in coral reef ecology), and the third is in her third year of undergraduate training with a major in Evolution and Ecology. We believe that working on this project helped stimulate their interest in science. Further, results from this project have led to one publication in preparation, one published peer-reviewed abstract, one course field and laboratory exercise, and 10 oral presentations at various local, state, and international conferences.

Peer-reviewed publication


Peer-reviewed abstracts


Course laboratory and field exercise

Zebra Mussel Size-Specific Excretion Rates. A coupled field and laboratory exercise developed for the course EEOB 655 – Limnology. The learning outcome for this exercise was for students to better conceptualize the importance for an invasive species, Dreissenid spp., in affecting processes (nutrient cycling) other than those it was originally hypothesized to affect (energy cycling by grazing large quantities of phytoplankton). In particular, this exercise calculated the nitrogen and phosphorus excretion rates of dreissenids based on their sizes for a sample either collected by the students or for a known density of mussels collected as part of this project.

Presentations


